Meta-analysis to predict sweating and respiration rates for *Bos indicus*, *Bos taurus*, and their crossbreds¹

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ABSTRACT: The overall objective of this work was to develop empirical equations from a meta-analysis study to be used to implement initial values in a mechanistic heat balance model. The meta-analysis was conducted to 1) develop prediction equations for sweating and respiration rate (SR, g m⁻² h⁻¹ and RR, breaths-min⁻¹, respectively) based on skin and body temperature (*T*ₘ and *T*ᵦ, °C, respectively) for different breed types: *Bos indicus*, *Bos taurus*, and their crossbreds, and 2) evaluate the fit of existing SR equations and the SR and RR equations (from objective 1) against independent data sets. Fourteen studies were collected for the SR analysis, 12 for fitting and 2 for evaluation. The fitted SR equations (Thompson model) for the 3 breeds types were *B. indicus*, SR = 0.085e⁰.²²*T*ₘ; *B. taurus*, SR = 0.75e⁰.₁₅*T*ₘ; and crossbreds, SR = 0.015e⁰.₂₅*T*ₘ. Twenty-three studies were collected for the RR analysis, 20 for fitting and 3 for evaluation. The fitted RR equations for the 3 breed types were *B. indicus*, RR = −1,660 + 43.8·*T*ₘ; *B. taurus*, RR = −1,385 + 37·*T*ₘ; and crossbreds, RR = −2,226 + 59·*T*ₘ. Three SR equations (Maia, McArthur, and Gatenby models) from the literature were evaluated against the Thompson model using the 14 studies. The McArthur model predicted SR within the correct range, but with an increased slope bias because the equation was linear and not the correct shape. The Maia model overpredicted SR for all breed types with the greatest overprediction being for crossbreds. The Gatenby model overpredicted SR for *B. taurus* (root mean square error of prediction = 506 g m⁻² h⁻¹), but was the best predictor for *B. indicus*. The Thompson model overpredicted SR for *B. indicus* (root mean square error of prediction ranged from 134 to 265 g m⁻² h⁻¹), but was the best predictor for *B. taurus* and crossbreds. The Thompson model was a good predictor for RR across all breed types. The meta-analysis showed that the Thompson model outperformed previous models for both RR and SR with the exception of the SR of *B. indicus*, which was best predicted by the Gatenby model.

Key words: *Bos indicus*, cattle, heat stress, meta-analysis, respiration rate, sweating rate

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INTRODUCTION

Heat stress is a serious problem for livestock production in warm regions. Heat-stressed cattle have increased basal metabolic rate yet decreased metabolic heat production because of decreased intake (Ames et al., 1971; Brown-Brandl et al., 2003; St-Pierre et al., 2003). Decreased intake is directly linked to decreased milk production in dairy cattle and decreased growth in beef cattle, resulting in large economic losses for the industries (Mitlöwner et al., 2001; Kadzere et al., 2002). However, heat stress is difficult to quantify in cattle; thus, a mathematical model that simulates heat balance in cattle and predicts heat stress would assist the dairy and beef industry in implementing mitigation strategies.

Several models have been developed to account for heat stress in cattle, among which are many 2 and 3 pool models (the pools represent body and skin, or body, skin, and coat heat content) that account for physiological responses (Mount and Brown, 1982; McArthur, 1987; McGovern and Bruce, 2000). These mechanistic models have limitations in that they are static or are not flexible enough, or both, to account for different climatic conditions and animal genotypes. evaporative heat loss through sweating and respiration are foremost among the functions that should be included in a mechanistic model. Many sweating and respiration rate (SR and RR, respectively) equations may be found in the literature (Gatenby, 1986; McArthur, 1987; Brown-Brandl et al., 2005b). Large differences exist among

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Table 1. Summary of the data collected by breed type

<table>
<thead>
<tr>
<th>Breed type</th>
<th>( T_b, ^\circ C )</th>
<th>( T_s, ^\circ C )</th>
<th>RR, breaths-min(^{-1})</th>
<th>SR, g·m(^{-2})·h(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>( B. taurus )</td>
<td>39.9</td>
<td>37.5 to 42.0</td>
<td>63.5</td>
<td>29.0 to 289</td>
</tr>
<tr>
<td>Crossbreds</td>
<td>39.1</td>
<td>38.3 to 40.8</td>
<td>36.5</td>
<td>29.0 to 39.4</td>
</tr>
<tr>
<td>( B. indicus )</td>
<td>39.2</td>
<td>38.0 to 40.9</td>
<td>49.1</td>
<td>16 to 125</td>
</tr>
</tbody>
</table>

\( T_b \) and \( T_s \) are body and skin temperatures, respectively. RR = respiration rate; SR = sweating rate.

References: Brody, 1956; Johnston et al., 1958; Taneja, 1958; Shrode et al., 1960; Brown and Motasem, 1965; Schleger and Turner, 1965; Murray, 1966; Hales and Findlay, 1968; Joshi et al., 1968; Allen et al., 1970; Gonyou et al., 1979; Seif et al., 1979; Egbunike et al., 1983; Finch, 1986; Gatenby, 1986; Hammond et al., 1996; Ahmed and ElAmin, 1997; Kasa, 1997; Gaughan et al., 1999; Brown-Brandl et al., 2005a; Maia et al., 2005; Smith et al., 2006; Gaughan et al., 2008; Scharf et al., 2008; McManus et al., 2009; Schütz et al., 2010.

A smaller proportion of articles containing SR data fit the inclusion criteria stated above compared with those containing RR data. The majority of the articles containing RR were for \( B. taurus \) dairy cattle (Holstein and Jerseys); therefore, only 25% of the \( B. taurus \) dairy cattle articles were randomly chosen and included in the data set.

The resulting data sets for SR and RR included data from many different cattle breeds, which were grouped into breed types to simplify the statistical analyses. Breed type was treated as a discrete variable and split into 3 groups, \( B. indicus \), \( B. taurus \), and their crossbreds. The crossbred cattle needed to be less than 75% of a specific breed type; otherwise the cattle were categorized as either \( B. taurus \) or \( B. indicus \). For each breed type, further classifications were applied according to purpose (i.e., dairy or beef) and adaptation (i.e., temperate or tropical). Table 1 shows the means and ranges of SR and RR from the data sets used to fit the models for the 3 breed types.

MATERIALS AND METHODS

This research was based on analyses of data obtained from the literature and did not involve the use of animals; therefore, Institutional Animal Care and Use Committee approval was not obtained.

Data Collection

The search for data was conducted using the following key words: cattle, heat stress, \( B. indicus \), steers, heifers, cows, sweating, cutaneous evaporation, and respiration. The search websites used were http://science-direct.com and http://scholar.google.com.

Air temperature, skin temperature, and body temperature were the variables most correlated with SR and RR and were included in the data set as well as breed characteristics (breed type, adaptation, and purpose), animal characteristics (age, BW, sex, and metabolic status) and number of animals per treatment. Breed types were defined as described below.

Most available data from studies were in tabular form, separated by treatment. However, if the data were only available in figures, Engauge Digitizer 2.15 was used to extract the data points (Mitchell, 2002). If the data points extracted originated from different climatic conditions (e.g., different air temperatures, solar radiation), as opposed to being temporally distributed, then each point was entered into the data set as a treatment mean.

Only experiments with a minimum of either SR or RR, and 1 of the following variables, air temperature, skin temperature, or body temperature, were included in the meta-analysis. In addition, the SR data had to be in a form that was convertible to grams-meter\(^{-2}\)·hour\(^{-1}\).
heifers were in heat chambers with incremental increases in air temperature from 18 to 46°C.

b. Thomas and Pearson (1986): This experiment measured SR and RR along with body and skin temperatures on 2 Brahman and 2 Brahman × Friesian animals. One Brahman was a cow, whereas the other animals were steers. Measurements were made with an air temperature of 33°C with the animals at rest, during exercise, and 30 min after exercising.

c. Brown-Brandl et al. (2003): This experiment measured RR and rectal temperature on 9 Angus × Hereford × Pinzgauer × Red Poll steers. The steers were in environmental chambers, with sinusoidal air temperatures in which the mean air temperature across treatments ranged from 18 to 34°C, with animal measurements taken every 15 min.

Statistical Analysis

The statistical analyses were conducted using R (R Development Core Team, 2009). Library lme4 was loaded for the statistical model, and the function applied was lmer, which is a mixed model analysis. Both SR and RR analyses treated study as a random effect, whereas all other variables were treated as fixed effects. In the SR analysis, the slope within study was also treated as a random effect along with the study intercept. The models in both analyses will be referred to as the Thompson models and will be evaluated based on criteria described in the Model Evaluation Equations section.

Model Evaluation Equations. The second objective of this research was to evaluate the newly developed equations for both SR and RR, along with previous equations for SR. The calculations to assess model fit followed Eq. [1] to [6] described by Tedeschi (2006), where \( y \) represents the observations, \( \bar{y} \) is the mean of the observations, \( \bar{Y} \) is the expected value of \( y \), and \( n \) is the number of observations (\( y \)).

\[
MB = \frac{\sum (y - \bar{Y})}{n}; \quad [1]
\]
\[
\text{MSEP} = \frac{\sum (y - \bar{Y})^2}{n}; \quad [2]
\]
\[
\text{bias} = \frac{\text{mean}(\bar{Y}) - \bar{y}}{\text{MSEP}}; \quad [3]
\]
\[
\text{slope} = \frac{(s_\bar{Y}^2 - s_y^2)}{\text{MSEP}}; \quad [4]
\]
\[
\text{random} = (1 - R^2) \cdot s_y^2 / \text{MSEP}; \quad [5]
\]
\[
\text{RMSEP} = \sqrt{\text{MSEP}}. \quad [6]
\]

The mean bias is denoted as MB; MSEP is the mean square error of prediction; bias, slope, and random are the proportions of error due to central tendency, regression, and disturbances, respectively; and RMSEP is the root mean square error of prediction. The terms bias, slope, and random can be explained as the proportions of MSEP and are good indicators of model fit. If the bias is large, then on average the model is either over- or underpredicting. An increased slope indicates a systematic error (i.e., the equation form does not adequately describe the data). An increased random indicates that the model is a good fit to the data, and the only error left is random, such as experimental error or differences in subjects or techniques (Tedeschi, 2006). The terms \( s_y \) and \( s_\bar{Y} \) represent the SD of the set of values \( y \) and \( \bar{Y} \), respectively, and the term mean(\( \bar{Y} \)) represents the mean of the set of values \( \bar{Y} \).

SR. A preliminary analysis of the SR data was conducted involving 3 main independent variables (air, skin, and body temperatures). Of these, only body and skin temperatures were assumed to be mechanistic drivers. Sweating rate was plotted against skin and body temperatures. Skin temperature was more closely related to SR than body temperature based on a visual inspection and preliminary model fits. Tanega (1958), Brown and Motasem (1965), Joshi et al. (1968), Allen et al. (1970), and Gatenby (1986) also found that SR was more highly correlated with skin than with body temperature. Therefore, subsequent statistical analyses used skin temperature as the independent variable and SR as the dependent variable (Figure 1), and all studies not containing these 2 measurements were excluded from the data set.

A statistical analysis conducted with purpose (dairy vs. beef) and adaptation (tropical vs. temperate) as the main effects, using the fixed effects test (this is an output of lmer function in R), showed that these were not significant; thus, they were not included in the model. A preliminary statistical analysis was conducted to test several models (linear, power, logistic, and exponential), which resulted in the following exponential equation to be the best fit for SR:

\[
\text{SR}_{ijk} = a_{ij} \cdot e^{(T_s \cdot b_j)} + \varepsilon_{ijk}, \quad [7]
\]

where \( \text{SR}_{ijk} \) is sweating rate (g·m\(^{-2}\)·h\(^{-1}\)), \( T_s \) is skin temperature (°C), \( a_{ij} \) and \( b_j \) are parameters, and \( \varepsilon_{ijk} \) is the error term. The index \( i \) represents breed type (\( i = 1, 2, 3 \)), \( j \) is the study (\( j = 1, \ldots, 12 \)), and \( k \) is the observation (\( k = 1, \ldots, n_{ij} \)), where \( n_{ij} \) is the observation number for the \( i \)th breed type of the \( j \)th study. The parameters \( a_{ij} \) and \( b_j \) account for breed type (\( Br_t^a \) and \( Br_t^b \)) and study effect (\( St_j^a \) and \( St_j^b \)), Eq. [8] and [9], where \( \mu^a \) and \( \mu^b \) are the constant values for parameters \( a_{ij} \) and \( b_j \), respectively. Parameter \( a_{ij} \) (g·m\(^{-2}\)·h\(^{-1}\)) represents the intercept, and \( b_j \) (°C\(^{-1}\)) represents the slope.
The superscripts \( a \) and \( b \) show that the variables \( \mu \), \( B_{ri} \), and \( S_{tj} \) are specific to the equations to calculate the variables \( a_{ij} \) and \( b_{ij} \). The breed effect, \( B_{ri} \), represents the effect of breed on the intercept, and \( B_{ri} \) represents the interaction between breed and skin temperature (breed type \( \times \) skin temperature). The study effects, \( S_{tj} \) and \( S_{tj} \), are random with a normal distribution: \( S_{tj} \) is the study intercept and \( S_{tj} \) is the study slope. Sweating rate (Eq. [7]) is only indexed on \( i \) for predictions and represents 3 different equations, one for each breed type with the respective variables (\( a \) and \( b \)) for each equation.

Equation [7] was implemented in R as a linear model through a natural log-transformation, which facilitated statistical analyses. Breed and study were both entered into the model as categorical variables. The resulting equation was treated as a mixed model (lmer; package: lme4) weighted by \( 1/n \) (SE was not available for all studies), with study as a random effect and breed and skin temperature as fixed effects.

**Combination Analysis.** A cross validation statistical analysis was implemented, in addition to other analyses. This involved recursively splitting the 12 data sets into 2 groups, fitting the model to 1 group and then evaluating it against the other group. The fitting group contained 8 data sets, whereas the evaluation group contained 4 data sets. All possible combinations of splitting the 12 data sets into subsets of 8 and 4 were analyzed. The statistical model (Eq. [7]) described above was implemented to fit the 8 data sets, and Eq. [1] to [6] were calculated to evaluate the model with the remaining 4 data sets.

**Goodness of Fit.** This analysis was undertaken to evaluate goodness of fit of the SR data from all 12 studies fitted to Eq. [7] and evaluated against 3 previously published equations. The existing equations (Eq. [10] to [12]) evaluated were from Gatenby (1986), McArthur (1987), and Maia et al. (2005). The models below were assessed as described in the Model Evaluation Equations section (Eq. [1] to [6]).

Gatenby: \[
SR = 3.6 \cdot e^{\frac{[T_s - T_0]}{B}},
\]

where \( T_0 \) is the threshold sweating temperature (°C), and \( B \) is a parameter. The values for \( T_0 \) and \( B \) are 32 and 1.58 for \( B. indicus \), 30.8 and 1.15 for \( B. taurus \), and 33.8 and 0.94 for crossbreds, respectively.

Maia: \[
SR = 91.97 \cdot e^{\frac{T_s - 33.11}{2.73}};
\]

McArthur: \[
SR = 14.4 + 65 \cdot (T_s - 33).
\]
Respiration Rate. A preliminary analysis of the data showed that RR was more highly correlated with body temperature than with skin temperature. This analysis was based on both a visual assessment of the data and model fits using a mixed model. Taneja (1958), Allen et al. (1970), Gatenby (1986), and Maia et al. (2005) all found a similarly stronger correlation of RR with body temperature than with skin temperature. An exponential relationship between skin temperature and RR was found, but fewer data points supported this relationship compared with body temperature and RR. The resulting analysis included 23 studies with both body temperature and RR (Figure 2) and of these studies, 20 were used to fit the model and 3 were used to test the model.

A preliminary statistical analysis was conducted to test several RR models (linear, power, logistic, and exponential), as was done for SR, and yielded the following linear equation as the best fit for RR:

\[
RR_{ijk} = c_{ij} + d_{ij} \cdot T_b + \varepsilon_{ijk}, \tag{13}
\]

where \(RR_{ijk}\) is respiration rate (breaths-min\(^{-1}\)), \(T_b\) is body temperature (°C), \(c_{ij}\) and \(d_{ij}\) are parameters, and \(\varepsilon_{ijk}\) is the error term (the indexing is similar to that described for Eq. [7], although study, \(j = 1, \ldots, 20\)). The parameters \(c_{ij}\) (breaths-min\(^{-1}\)) and \(d_{ij}\) (breaths-min\(^{-1}\)°C \(^{-1}\)) account for breed type (\(B_{rt}^c\) and \(B_{rb}^c\)) and study effect (\(St_j^c\); Eq. [14] and [15]):

\[
c_{ij} = \mu^c + B_{rt}^c + St_j^c, \tag{14}
\]

\[
d_{ij} = \mu^d + B_{rt}^d. \tag{15}
\]

The symbol \(B_{rt}^c\) represents the effect of breed on the intercept and \(B_{rt}^d\) represents the interaction between breed and body temperature (breed type x body temperature). The study effect (\(St_j^c\)) is random, with a distribution \(St_j^c \sim N(0, \sigma^2)\) that only affects the intercept (Eq. [14]) and not the slope (Eq. [15]). The slope within study is not set as random because the equation is linear with a constant slope across all \(T_b\) values. Respiration rate (Eq. [13]) is indexed only on \(i\) for predictions and represents 3 different equations, one for each breed type, with the respective parameters (\(c\) and \(d\)) for each equation.

Equation [13] was implemented in R directly as a linear mixed model (lmer; package: lme4) weighted by \(1/n\) (SE was not available for all studies), with study as a random effect and breed and body temperature as fixed effects. The model was then evaluated against test data sets using the same output calculations as those used in the SR analysis (Eq. [1] to [6]).

### RESULTS AND DISCUSSION

#### Model Development

Sweating Rate. The fixed effects, breed, skin temperature, and their interaction (Eq. [7] to [9]), were significant (\(P = 0.005, <0.0001,\) and 0.0007, respectively) in the SR analysis. The resulting equations for the SR model were as follows: \(B.\min\), \(SR = 0.085e^{0.22T_r}\) (RMSEP = 194 g-m\(^{-2}\)-h\(^{-1}\)); \(B.\ taurus\), \(SR = 0.76e^{0.15T_r}\) (RMSEP = 174 g-m\(^{-2}\)-h\(^{-1}\)); and crossbreds, \(SR = 0.015e^{0.25T_r}\) (RMSEP = 148 g-m\(^{-2}\)-h\(^{-1}\)).

Figure 3 shows the fit equations (Thompson model) for the 3 breed types calculated with Eq. [7]. Bos in-
dicus had greater SR than both B. taurus and crossbreds at all skin temperatures. B. taurus had greater SR than crossbreds at skin temperatures below 36.5°C, but above this temperature crossbreds had greater SR. Studies demonstrate that B. taurus are less adapted to hot conditions and at decreased air temperatures have a greater SR than B. indicus (Thompson et al., 1953; Allen, 1962; Finch, 1985). B. indicus exhibit a decreased SR compared with B. taurus at the same environmental temperature, but not the same skin temperature, because of a decreased susceptibility to heat stress. At the same skin temperatures, B. taurus cattle will sweat less than B. indicus due to the effects of vasodilation. As an animal becomes more heat stressed, cutaneous vasodilation increases, which leads to an increase in skin temperature (Finch, 1986). Finch (1985) found that B. indicus have increased resistance to environmental heat, and thus, cooler skin temperatures compared with B. taurus. Therefore, at the same environmental temperature, a B. taurus under heat stress can have a greater skin temperature and greater SR than a B. indicus.

The differences in SR among breeds may be attributed to physiological differences in sweat gland size, shape, and density. Carvalho et al. (1995) found that B. indicus have larger sweat glands than B. taurus. Nay and Heyman (1956) found that B. indicus not only have larger sweat glands, but also a greater density of sweat glands than B. taurus, which is directly associated with an increase in SR (Pan et al., 1969). Yeates et al. (1975) found that the “baggy” type sweat glands of B. indicus are associated with heat tolerance compared with the “narrow, coiled” glands of B. taurus. The combination of these anatomical and physiological differences results in an increased SR capacity for B. indicus, as was found in the literature (Allen et al., 1963; Buvanendran et al., 1992; Gaughan et al., 1999).

Similar to this study, Finch et al. (1982) found that as body and air temperatures rose, crossbreds, which initially sweat less than B. taurus, increased their SR above that of B. taurus, but not of B. indicus. Results were similar to Hansen (2004) because crossbreds were intermediary between B. indicus and B. taurus in terms of physiological adaptations to heat stress. Allen (1962) showed that crossbreds surpassed B. taurus in SR when skin temperature increased above 34.5°C, but contradicting the results in this study, B. indicus had the least SR at skin temperatures greater than 34.5°C.

**Respiration Rate.** Body temperature, breed, and their interaction were all significant (P < 0.0001) in the model fit. The resulting equations for the RR model were B. indicus, RR = −1,660 + 44·Tₕ (RMSEP = 29 breaths·min⁻¹); B. taurus, RR = −1,385 + 37·Tₕ (RMSEP = 35 breaths·min⁻¹); crossbreds, RR = −2,226 + 59·Tₕ (RMSEP = 44 breaths·min⁻¹). Figure 4 shows the fit equations (from Eq. [13]) of RR vs. body temperature for the 3 breed types. B. indicus had the least RR across all body temperatures. Below a body temperature of 39.5°C, B. taurus had greater RR than crossbreds, whereas above this temperature, crossbreds had greater RR. The fitted equations for RR are in agreement with many experiments, which show B. indicus have a reduced RR compared with both crossbreds and B. taurus (Buvanendran et al., 1992; McMamus et al., 2009).

Figures 3 and 4 are complementary in that when a breed type cannot expel substantial heat through SR, the RR of that breed type increases. B. indicus can lose a large amount of heat through sweating; therefore, the breed type is less dependent on respiration and has the least RR across all body temperatures. On the con-

![Figure 3](image-url)

**Figure 3.** Sweating rates (SR; g·m⁻²·h⁻¹) predicted from skin temperature (Tₛ; °C) by the Thompson model (Eq. [7]). Equations: Bos taurus, SR = 0.75e⁰.₁₅Tₛ; crossbreds, SR = 0.015e⁰.₂₅Tₛ; Bos indicus, SR = 0.085e⁰.₂₂Tₛ.

![Figure 4](image-url)

**Figure 4.** Respiration rates (RR; breaths·min⁻¹) predicted from body temperature (Tₖ; °C) by the Thompson model (Eq. [13]). Equations: Bos taurus, RR = −1,385 + 37·Tₖ; crossbreds, RR = −2,226 + 59·Tₖ; Bos indicus, RR = −1,660 + 44·Tₖ.
Meta-analysis to predict sweating and respiration rates

**Model Evaluation: Sweating Rate**

**Combination Analysis.** The combination analysis evaluated the predictive ability of the model in the absence of an independent test data set. The mean RMSEP was 216.2 g·m⁻²·h⁻¹, which was only slightly larger than the RMSEP of the model fit to the entire data set (179.8 g·m⁻²·h⁻¹). The assumption made in this analysis was that the entire model would predict against independent data with an RMSEP falling within the same distribution as that obtained from this analysis. The RMSEP from the entire model tested against independent data (in the Challenge section) was generally much less than the RMSEP found from this analysis but did fall within the distribution. This technique is useful when there are few present data sets, but it does not replace the following 2 techniques to evaluate the SR equations.

**Goodness of Fit.** The goodness of fit of the SR model (created with the 12 studies) is shown in Table 2. The Gatenby model was developed with data from *B. taurus*, *B. indicus*, and crossbreds. The average skin temperature Gatenby used to fit the *B. indicus* equation was 35.0°C which was 0.6°C greater than the average used to fit the Thompson model for *B. indicus*, but 1.5°C less than the average for *B. taurus* and crossbreds. Therefore, the Gatenby model greatly outpredicted SR at skin temperatures above the range in which the model was fit; thus the RMSEP is the largest for this model (4,106.6 g·m⁻²·h⁻¹). The average skin temperature used to fit the Maia model was 32.7°C, which was from lactating Holstein cows. This temperature value was much less than the average from fit data set because instead of measuring skin temperature, Maia et al. (2005) measured coat surface temperature. The coat surface temperature is usually less than both skin and body temperature and may explain why the predictions of the Maia model were uniformly high across all breed types. The McArthur model was linear and was within the correct SR range near the average skin temperatures, but the model consistently underpredicted SR at high and low skin temperatures. In addition, the McArthur model resulted in negative SR values at skin temperatures below 32.8°C, which is within the normal skin temperature range found for all breed types.

The total random error in the SR data is very large and comes from 2 main sources. One of these sources is the location on the animal chosen to measure SR. Pan et al. (1969) found that compared with the loin, other areas such as the front of the shoulder can produce 60% more sweat per hour. Gatenby (1980) found that the backs of zebu cattle can sweat 3 times as much as their bellies. Gatenby (1980) also found a local effect of skin temperature, where the skin area of an animal that received direct sunlight sweated more than other areas. Unfortunately, some of the studies used in this analysis did not state the location on the animal where SR was measured. The differences in location of measurement between studies were accounted for by including study as a random effect in the meta-analysis. The other source of error is the experimental method implemented to measure SR, which varied greatly in the data sets collected for the meta-analysis. Some methods involved elaborate ventilation mechanisms, whereas others used paper discs with which SR can be calculated based on the speed at which the discs change color. These different methods all have different errors associated with them, in addition to other sources of error such as those from animal handling and welfare. A stressed animal may have an increased SR, yet in most studies and treatments the level of stress of the animal was not mentioned or quantified. Due to all of these factors, the relatively poor fits achieved by the meta-analysis for all 3 breed types were considered to be the best that could be achieved for the purposes of developing the mechanistic heat balance model.

All of the models greatly overpredicted at high values, with the maximum overprediction being Maia (1,336 g·m⁻²·h⁻¹) and Gatenby (27,549 g·m⁻²·h⁻¹). The corresponding mean biases of these models, which demonstrate the overprediction, were −106.0 and −906.3 g·m⁻²·h⁻¹, respectively (Table 2). The McArthur model did not greatly over- or underpredict (mean bias = 68.0 g·m⁻²·h⁻¹), but gave infeasible (negative) solutions (the minimum prediction being −500 g·m⁻²·h⁻¹). The Thompson model yielded the least RMSEP (179.8 g·m⁻²·h⁻¹) and for this data set was superior to the previous models.

**Challenge.** The Gatenby and Maia models greatly overpredicted SR when evaluated against the Allen

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**Table 2. Goodness of fit for the 4 models of sweating rate tested against the fit data set**

<table>
<thead>
<tr>
<th>Model</th>
<th>Mean bias, g·m⁻²·h⁻¹</th>
<th>RMSEP, g·m⁻²·h⁻¹</th>
<th>R²</th>
<th>Bias</th>
<th>Slope</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gatenby</td>
<td>−906.3</td>
<td>4,106.6</td>
<td>0.019</td>
<td>0.049</td>
<td>0.949</td>
<td>0.002</td>
</tr>
<tr>
<td>Maia</td>
<td>−106.0</td>
<td>297.6</td>
<td>0.214</td>
<td>0.127</td>
<td>0.578</td>
<td>0.295</td>
</tr>
<tr>
<td>McArthur</td>
<td>68.0</td>
<td>181.6</td>
<td>0.294</td>
<td>0.140</td>
<td>0.148</td>
<td>0.712</td>
</tr>
<tr>
<td>Thompson</td>
<td>88.5</td>
<td>179.8</td>
<td>0.265</td>
<td>0.242</td>
<td>0.002</td>
<td>0.756</td>
</tr>
</tbody>
</table>

1RMSEP is the root mean squared prediction error. The error terms (bias, slope, and random) are dimensionless and sum to 1.
(1962) data set, as indicated in Table 3 by a negative mean bias. The Gatenby model was created with an average skin temperature less than the skin temperature of all breed types in the data set in Allen (1962), which may have led to the overpredicted SR for B. taurus and crossbreds. On the other hand, the Gatenby model was the only model that underpredicted SR for the B. indicus cattle from the Allen (1962) data set (by an average of 50 g·m⁻²·h⁻¹). The Maia model overpredicted SR for all 3 breed types and consistently had one-third of the error as slope. The exponential equation of the Maia model increased too sharply at high skin temperatures, resulting in large overpredictions. The McArthur model had a reduced bias across all breed types, but had a consistently greater slope (Table 3). This indicated that the model was in the correct range of SR for a given skin temperature, but that the shape of the model did not fit the data over the skin temperature range.

For B. taurus and crossbreds, the Thompson model performed better than the other models having most of the error in the random component (random). The Thompson model for B. indicus. The Maia model overpredicted SR, and the McArthur model predicted negative numbers for both the breed types of the Thomas and Pearson (1986) data set. The McArthur model had low predictions, so its predicted values fell within the range of the data, but its shape did not fit the data, which resulted in a large slope.

Overall, the Thompson model was the best predictor of SR for B. taurus and crossbreds and the Gatenby model was best predictor for B. indicus when evaluating the models against the Allen (1962) and Thomas and Pearson (1986) data sets.

### Model Evaluation: Respiration Rate

The RR model fit the data well when evaluated against independent data sets and the majority of the error for all the data sets was random (Table 5). The RMSEP was small enough that it should not affect the predictive ability of the model (10.7 to 16.7 breaths·min⁻¹). The RR and SR models were developed for use in an overall heat balance model; thus, their predictions should not have errors large enough to shift the heat balance of the animal.

The proportion of RMSEP of the mean RR is 0.20, which means that actual RR may range from 11 to 17 breaths·min⁻¹ when the animal is under normal climate conditions. The heat loss through respiratory evaporation is around 7.5% of their total body heat loss un-

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### Table 3. The results of the 4 sweating rate models tested against the Allen (1962) data set

<table>
<thead>
<tr>
<th>Breed type</th>
<th>Model</th>
<th>Mean bias, g·m⁻²·h⁻¹</th>
<th>RMSEP,¹ g·m⁻²·h⁻¹</th>
<th>R²</th>
<th>Bias</th>
<th>Slope</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. taurus</td>
<td>Gatenby</td>
<td>−258.1</td>
<td>505.9</td>
<td>0.586</td>
<td>0.258</td>
<td>0.737</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Maia</td>
<td>−107.7</td>
<td>142.9</td>
<td>0.750</td>
<td>0.564</td>
<td>0.396</td>
<td>0.040</td>
</tr>
<tr>
<td></td>
<td>McArthur</td>
<td>−28.0</td>
<td>72.3</td>
<td>0.798</td>
<td>0.148</td>
<td>0.726</td>
<td>0.125</td>
</tr>
<tr>
<td></td>
<td>Thompson</td>
<td>−13.5</td>
<td>33.8</td>
<td>0.793</td>
<td>0.160</td>
<td>0.246</td>
<td>0.594</td>
</tr>
<tr>
<td>Crossbred</td>
<td>Gatenby</td>
<td>36.2</td>
<td>64.8</td>
<td>0.513</td>
<td>0.307</td>
<td>0.258</td>
<td>0.435</td>
</tr>
<tr>
<td></td>
<td>Maia</td>
<td>−140.9</td>
<td>169.9</td>
<td>0.701</td>
<td>0.683</td>
<td>0.278</td>
<td>0.039</td>
</tr>
<tr>
<td></td>
<td>McArthur</td>
<td>−60.3</td>
<td>92.6</td>
<td>0.713</td>
<td>0.418</td>
<td>0.456</td>
<td>0.126</td>
</tr>
<tr>
<td></td>
<td>Thompson</td>
<td>−34.0</td>
<td>47.0</td>
<td>0.717</td>
<td>0.517</td>
<td>0.001</td>
<td>0.482</td>
</tr>
<tr>
<td>B. indicus</td>
<td>Gatenby</td>
<td>49.7</td>
<td>60.5</td>
<td>0.673</td>
<td>0.673</td>
<td>0.011</td>
<td>0.316</td>
</tr>
<tr>
<td></td>
<td>Maia</td>
<td>−133.6</td>
<td>165.6</td>
<td>0.667</td>
<td>0.648</td>
<td>0.309</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td>McArthur</td>
<td>−52.8</td>
<td>96.2</td>
<td>0.574</td>
<td>0.298</td>
<td>0.540</td>
<td>0.162</td>
</tr>
<tr>
<td></td>
<td>Thompson</td>
<td>−124.4</td>
<td>134.3</td>
<td>0.643</td>
<td>0.856</td>
<td>0.074</td>
<td>0.070</td>
</tr>
</tbody>
</table>

¹RMSEP is the root mean squared prediction error. The error terms (bias, slope, and random) are dimensionless and sum to 1.

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### Table 4. The results of the 4 sweating rate models tested against the Thomas and Pearson (1986) data set

<table>
<thead>
<tr>
<th>Breed type</th>
<th>Model</th>
<th>Mean bias, g·m⁻²·h⁻¹</th>
<th>RMSEP,¹ g·m⁻²·h⁻¹</th>
<th>R²</th>
<th>Bias</th>
<th>Slope</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crossbred</td>
<td>Gatenby</td>
<td>−267.1</td>
<td>449.4</td>
<td>0.802</td>
<td>0.327</td>
<td>0.671</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Maia</td>
<td>−339.0</td>
<td>424.2</td>
<td>0.841</td>
<td>0.611</td>
<td>0.387</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>McArthur</td>
<td>−135.7</td>
<td>191.3</td>
<td>0.723</td>
<td>0.473</td>
<td>0.509</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>Thompson</td>
<td>−91.6</td>
<td>109.8</td>
<td>0.819</td>
<td>0.671</td>
<td>0.292</td>
<td>0.037</td>
</tr>
<tr>
<td>B. indicus</td>
<td>Gatenby</td>
<td>−65.7</td>
<td>97.8</td>
<td>0.936</td>
<td>0.423</td>
<td>0.568</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Maia</td>
<td>−336.2</td>
<td>416.3</td>
<td>0.966</td>
<td>0.625</td>
<td>0.375</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>McArthur</td>
<td>−140.5</td>
<td>220.0</td>
<td>0.892</td>
<td>0.380</td>
<td>0.617</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Thompson</td>
<td>−236.7</td>
<td>265.0</td>
<td>0.958</td>
<td>0.779</td>
<td>0.221</td>
<td>0.001</td>
</tr>
</tbody>
</table>

¹RMSEP is the root mean squared prediction error. The error terms (bias, slope, and random) are dimensionless and sum to 1.
under normal climate conditions, which reduces the error from RR to 1.5% of total body heat loss (Blaxter and Wainman, 1961). The contribution of RR to evaporative heat loss is around 15% as RR reaches a maximum of around 250 breaths min⁻¹, which results in the error from RR of 3.0% of total evaporative heat flow (Kibler and Brody, 1952; Blaxter and Wainman, 1961). This level of error is not expected to affect the mechanistic heat balance model. Therefore, the Thompson model for RR was considered an adequate predictor for all 3 breed types.

In conclusion, the RR equations (Figure 4) presented here are excellent predictors for all 3 breed types. Furthermore, the SR equations (Figure 3) for B. taurus and crossbreds are improved from previously published equations because of the reduced RMSEP and mean bias. Despite this, it is still advised to use the Gatenby equation to predict SR for B. indicus.

Further experimentation may provide a better understanding and a possible quantification of the random component (Eq 5) for prediction SR. This experimentation would also require that a common, reliable method be defined for either collecting data on SR, or adjusting data based on different measurement techniques. Many studies have measured RR in B. taurus dairy cattle, but far fewer in B. indicus. An extensive comparison study using different breed types and collecting skin and body temperatures and SR and RR would be a valuable contribution because there are such large between-study errors. Careful experimental design would be required to reduce the within-study error and to control the large variation due to methodology.

LITERATURE CITED


Table 5. Respiration rate predicted by the Thompson model evaluated against 3 independent data sets

<table>
<thead>
<tr>
<th>Reference</th>
<th>Mean bias, breaths-min⁻¹</th>
<th>RMSEP breaths-min⁻¹</th>
<th>R²</th>
<th>Bias</th>
<th>Slope</th>
<th>Random</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown-Brandl et al. (2003)</td>
<td>-3.66</td>
<td>10.71</td>
<td>0.836</td>
<td>0.116</td>
<td>0.027</td>
<td>0.856</td>
</tr>
<tr>
<td>Allen (1962)</td>
<td>-1.85</td>
<td>16.67</td>
<td>0.573</td>
<td>0.012</td>
<td>0.020</td>
<td>0.968</td>
</tr>
<tr>
<td>Thomas and Pearson (1986)</td>
<td>-4.99</td>
<td>12.47</td>
<td>0.931</td>
<td>0.102</td>
<td>0.149</td>
<td>0.749</td>
</tr>
</tbody>
</table>

¹The data sets include all the breed types evaluated within each experiment.

²RMSEP is the root mean squared prediction error. The error terms (bias, slope, and random) are dimensionless and sum to 1.


